

## FORAGING OF BUMBLE BEES: THE EFFECT OF OTHER INDIVIDUALS

Douglass H. Morse

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### Introduction

Few experimental studies have been published upon the role that direct interactions play in niche partitioning under natural conditions, and even in these cases the mechanisms causing partitioning have seldom been reported (Kikuchi, 1965; Grant, 1970; Colwell and Fuentes, 1975; Morse, 1977). Therefore, I elected to explore this question, using a system which would readily permit me to study the basis for niche-shifting both rigorously and realistically. For this effort I chose a group of bumble bees (*Bombus* spp.: Apidae) that inhabit fields and other open places in the northeastern United States. This is part of a larger study upon foraging behavior and predator avoidance by bumble bees. The bumble bees, as I will demonstrate, provide the necessary criteria for testing both rigorously and realistically the hypothesis that an individual changes its foraging patterns in response to another species, and to investigate the basis for this change. Perhaps even more important, given that the individuals of an area concentrate on localized food sources, it becomes possible to assess the importance of the different species upon each other.

Here I present the results of several field experiments testing the effects of *Bombus ternarius* Say and *B. terricola* Kirby on each others' foraging on goldenrod (*Solidago juncea* and *S. canadensis*). I further compare them with observations made upon individuals, in many cases the same ones, that foraged unrestrained on similar flowers.

Bumble bees typically walk along the branches of these plume-like inflorescences gathering nectar from the florets. Any individual can feed from any of these florets and can also hang from the pendant tips of the branches if these branches will not otherwise support its weight. Most individuals forage for nectar, although they may acquire considerable amounts of pollen at the same time, as is easily witnessed by their characteristic bright orange corbiculae.

### Methods

At the start of an experiment I placed a screen-covered cage of about one m<sup>3</sup> over a clump of goldenrod, which had 8-12 stalks with inflorescences. These flowers were left uncovered at all times when experiments were not being run, therefore keeping nectar volumes consistent with those elsewhere in the field. A bee was released into the cage from the bottom. After

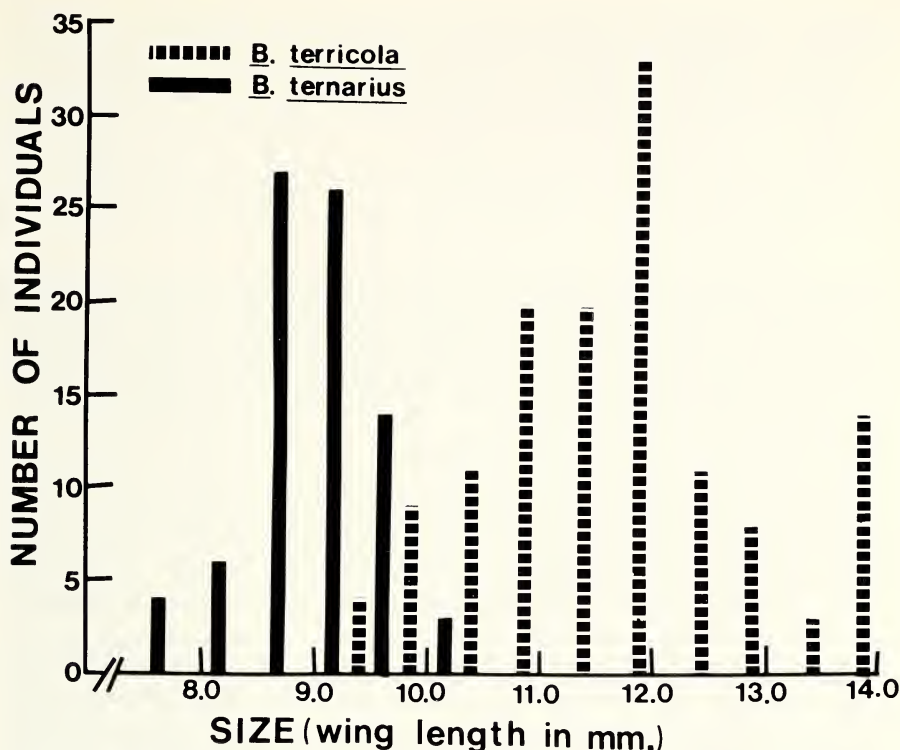


Fig. 1. Size of bumble bee workers in study area.

allowing it to forage for 30 s I counted the positions of the next 50 florets visited: whether they were located in the proximal, medial, or distal parts of the branches constituting the inflorescence (Morse, 1977). I scored each proximal observation 3, each medial one 2, and each distal one 1. Thus, any individual could receive a score as high as 150 or as low as 50. Simultaneously, I measured the time required by the bee to visit the 50 florets. About two-thirds of the individuals would readily forage under these circumstances. Those that would not forage were released from the cage, and new individuals were substituted for them.

I then introduced other bees in various combinations and allowed all individuals to forage in the cage for three minutes, which should insure that they were aware of each others' presence. Then I measured the foraging patterns of the first-introduced individual in the same way that I did several minutes earlier. For controls I ran experiments similar to those just outlined, except that I did not introduce additional bees prior to the second set of observations. Typically I ran 10 or more replicates for each set of experiments.

Table 1. Percentages of common bumble bees (*Bombus:Apidae*) in study area.

Year	Number of counts	<i>B. terricola</i>	<i>B. ternarius</i>	<i>B. vagans</i>
1975	15	67.2	17.3	15.5
1976	7	50.6	21.5	27.9
1977	12	79.0	10.5	10.5

To test for the possibility of cage effects I compared data gathered in the experiments with similar observations that I made of free-ranging individuals in the field. The observations of free-ranging bees were made upon the same marked individuals that were tested in the cages.

### Results

*Abundance and size of the bumble bees.*—*Bombus ternarius* and *B. terricola* are two of the commonest large pollinators of goldenrod along the Maine coast, where I conducted this study. *Bombus ternarius* workers are much smaller than those of *B. terricola* on the average (Fig. 1), although some overlap occurs.

A third species of bumble bee, *B. vagans* Smith, occurs in numbers comparable to those of *B. ternarius* (Table 1), but after the early part of the goldenrod season its numbers decline. In addition, yellowjackets, *Vespula* spp., and syrphid flies, primarily *Toxomerus marginatus* (Say), are often in attendance.

*Foraging locations.*—When *B. ternarius* workers were run in these experiments with larger *B. terricola* workers, the *ternarius* workers foraged more distally than they did when alone (Table 2). This pattern held without exception in the tests using three *terricola* workers. In experiments using a single *terricola*, a trend occurred for *ternarius* to forage more peripherally with the *terricola* than when alone, but this difference was not significant at the 0.05 level.

Table 2. Foraging scores of *Bombus ternarius* workers on 50 florets of goldenrod.

Treatment	n	score $\pm$ 1 SE <sub>m</sub>	P <sup>a</sup>
Before <i>Bombus terricola</i> added	12	90.4 $\pm$ 1.9	<0.003
No <i>B. terricola</i> added, 5 min later		99.1 $\pm$ 3.0	
Before <i>B. terricola</i> added	10	96.5 $\pm$ 1.6	>0.05
After one <i>B. terricola</i> added		90.4 $\pm$ 3.1	
Before <i>B. terricola</i> added	10	96.1 $\pm$ 1.7	<0.003
After three <i>B. terricola</i> added		79.4 $\pm$ 1.8	

<sup>a</sup> One-tailed Wilcoxon Test.

Table 3. Foraging scores of *Bombus ternarius* workers on 50 florets of goldenrod.

Treatment	<i>n</i>	score $\pm$ 1 SE <sub>m</sub>	<i>P</i> <sup>a</sup>
Before <i>Bombus terricola</i> added		96.4 $\pm$ 2.1	>0.05
Flying free in field		92.9 $\pm$ 2.8	

<sup>a</sup> One-tailed Wilcoxon Test.

To insure that these changes were not simply a function of the time that individuals had been feeding on a clump of goldenrod, I compared the foraging patterns of individuals that had been in the cage for several minutes with the patterns that they exhibited shortly after introduction. A significant tendency actually occurred to forage more medially after having been in the cage for this period of time. Thus, the results obtained from introducing *terricola* were conservative, in that the peripheral shifts observed counteracted a tendency to forage more medially after working on a clump of goldenrod for several minutes. These three sets of data (0, 1, 3 *terricola* added) differ highly significantly among themselves ( $P < 0.001$ ) in a Kruskal-Wallis, one-tailed analysis of variance.

The replicates from the experiments in which one *terricola* was added were composed of two types of responses: cases in which sizeable shifts occurred to more distal locations after a *terricola* worker was introduced, and cases where slight (and probably random) shifts occurred either in a distal or proximal direction (+1, -1, +3, +6, +8, -8, -9, -18, -20, -23). While I did not record precise observations on the location of the two performers in these experiments, in at least two cases where no marked shifts occurred the *ternarius* and *terricola* foraged at the opposite extremities of the clump of goldenrod, and in at least three cases where marked foraging shifts occurred the individuals foraged close to each other at least half of the time. More observations of this sort are needed.

Several individuals tested in the cages were also observed when in the field, and similar data were obtained. These individuals did not feed in significantly different locations from where they foraged when in the cages (Table 3).

To test the effect of *ternarius* upon the foraging of large *terricola* I ran similar tests in which a large *terricola* was first allowed to forage and then a *ternarius* worker was added. As a control I ran the *terricola* in the absence of *ternarius*, similarly to the reciprocal experiments.

Large *terricola* showed no tendency to change their foraging patterns when in the presence of *ternarius* (Table 4). Neither did a tendency occur for them to change their foraging patterns in the cages after a period of time had elapsed (Table 4). I did not run large *terricola* workers against three *ternarius* workers because I did not observe any combinations of free-ranging bees on goldenrod clumps that approached this ratio.



Table 4. Foraging scores of *Bombus terricola* workers on 50 florets of goldenrod.

Treatment	<i>n</i>	score $\pm$ 1 SE <sub>m</sub>	<i>P</i> <sup>a</sup>
Before <i>Bombus ternarius</i> added	9	102.3 $\pm$ 1.9	>0.05
No <i>B. ternarius</i> added, 5 min later		102.4 $\pm$ 2.2	
Before <i>B. ternarius</i> added	10	106.4 $\pm$ 2.2	>0.05
After one <i>B. ternarius</i> added		105.0 $\pm$ 2.9	

<sup>a</sup> One-tailed Wilcoxon Test.

*Rate of foraging.*—What is the cost to *ternarius* of *terricola*'s presence? One way to determine this cost is to measure the time required for *ternarius* to forage in the different areas. I assume that handling time per floret is solely a function of the time required for an individual to position itself and to probe a floret with its proboscis. Since individual goldenrod florets produce extremely small volumes of nectar (Heinrich, 1976), the amount of liquid potentially available should be absorbed instantly through capillary action (see Inouye, 1976).

No significant difference existed in the overall rates at which *ternarius* foraged by themselves in the initial runs and afterward in the presence of one *terricola*, three *terricola*, or by themselves (Table 5). When *ternarius* foraged in their initial runs there was no correlation between their rate of visiting florets and where the florets were located on the goldenrod. However, when with three *terricola*, those *ternarius* individuals foraging most distally visited florets at a significantly greater rate than did those feeding more proximally (Fig. 2). Those *ternarius* individuals foraging with a single *terricola* showed a slight but non-significant trend to forage most rapidly when in a distal position (Fig. 2). When tested against themselves five minutes after the first runs, distally foraging *ternarius* tended to forage more slowly, although not significantly so, than did individuals foraging more proximally. These three sets of data points differ highly

Table 5. Foraging rates (s) of *Bombus ternarius* workers on 50 florets of goldenrod.

Treatment	<i>n</i>	<i>s</i> $\pm$ 1 SE <sub>m</sub>	<i>P</i> <sup>a</sup>
Before <i>Bombus terricola</i> added	12	120.8 $\pm$ 5.8	>0.05
No <i>B. terricola</i> added, 5 min later		113.5 $\pm$ 5.1	
Before <i>B. terricola</i> added	10	78.2 $\pm$ 3.9	>0.05
After one <i>B. terricola</i> added		84.4 $\pm$ 2.3	
Before <i>B. terricola</i> added	12	110.2 $\pm$ 5.5	>0.05
After three <i>B. terricola</i> added		115.3 $\pm$ 6.7	

<sup>a</sup> One-tailed Wilcoxon Test.

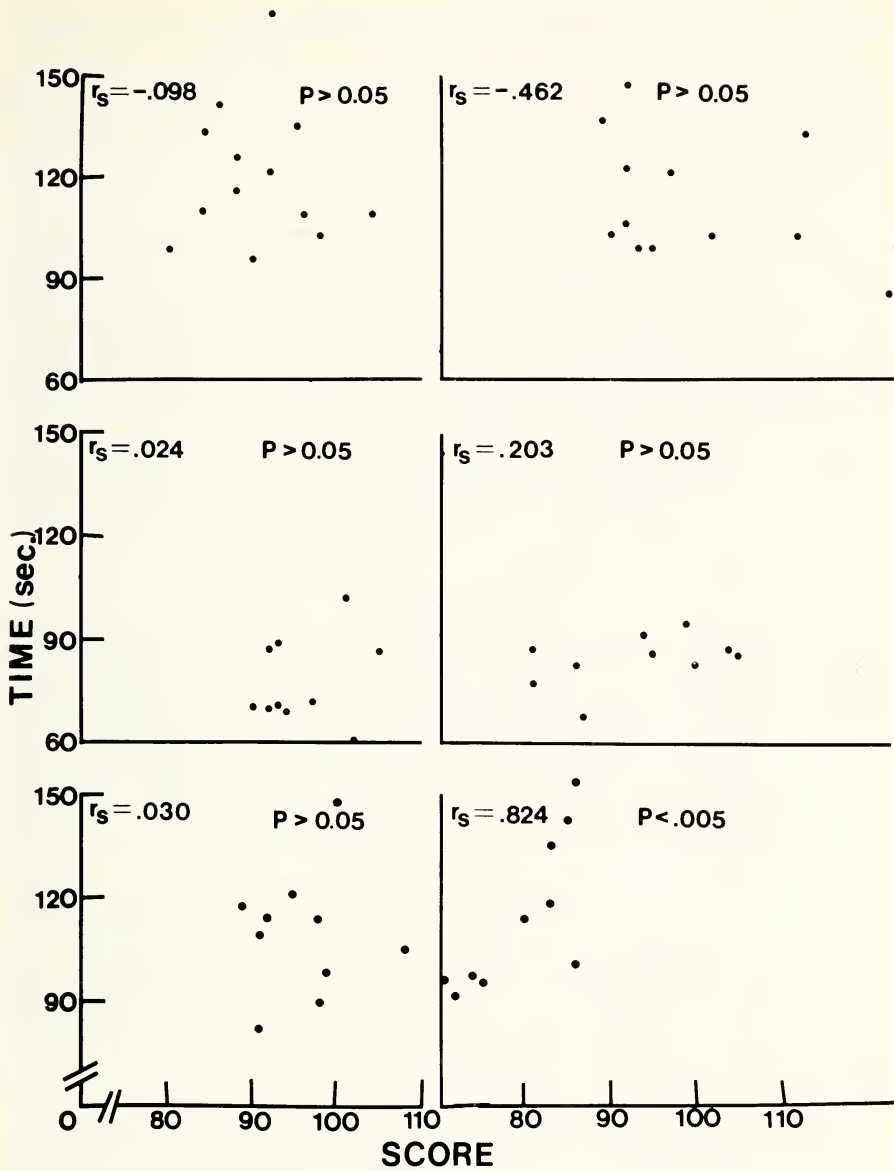


Fig. 2. Correlation between position on inflorescence and time required for *Bombus ternarius* workers to visit 50 florets. A-C = foraging patterns of *B. ternarius* alone shortly after introduction to test cage; D = foraging pattern of *B. ternarius* plotted in A five minutes later, with no *B. terricola* added; E = foraging pattern of *B. ternarius* plotted in B after one *B. terricola* added; F = foraging pattern of *B. ternarius* plotted in C after three *B. terricola* added. Significance levels refer to one-tailed Spearman Rank-Correlation Tests in each case.

Table 6. Foraging rates (s) of *Bombus ternarius* workers on 50 florets of goldenrod.

Treatment	n	s $\pm$ 1 SE <sub>m</sub>	P <sup>a</sup>
Before <i>Bombus terricola</i> added	12	109.8 $\pm$ 4.5	>0.05
Flying free in field		99.8 $\pm$ 5.4	

<sup>a</sup> One-tailed Wilcoxon Test.

significantly among themselves ( $P < 0.001$  in a Kruskal-Wallis, one-tailed analysis of variance), strengthening the initial observation that the best opportunity for rapid foraging by *ternarius* is in the distal areas when *terricola* is present in high densities. Although *ternarius* foraged somewhat more rapidly in the field than in cages, considerable scatter occurred, and the differences were not significant (Table 6).

Large *terricola* workers foraged at the same rate with a single *ternarius* that they did when by themselves (Table 7). Neither did they significantly change their foraging rates after being alone in the cage for several minutes (Table 7).

### Discussion

These results support the hypothesis that large *terricola* spatially displaced *ternarius*. The effect was most pronounced when *terricola* were at high, although not unnaturally high, densities. When *terricola* were at lower densities, crowding was apparently not high enough to produce this effect in every case. *Bombus ternarius* that came in close contact with large *terricola* workers under the latter circumstances responded in the same way that they did in the high-density runs.

*Bombus ternarius* did not noticeably affect the foraging of *terricola*. Given the usual social superiority of large individuals over small (Morse, 1974), this result is not surprising, but one that cannot simply be assumed.

The results further indicated that *ternarius* foraged with equal facility on all parts of the inflorescence when by itself. However, when with large numbers of *terricola* it retained this rate only when concentrating its activities on the distal parts of the inflorescences.

Table 7. Foraging rates (s) of *Bombus terricola* workers on 50 florets of goldenrod.

Treatment	n	s $\pm$ 1 SE <sub>m</sub>	P <sup>a</sup>
Before <i>Bombus ternarius</i> added	10	89.4 $\pm$ 3.8	>0.05
No <i>B. ternarius</i> added, 5 min later		93.3 $\pm$ 3.3	
Before <i>B. ternarius</i> added	9	103.8 $\pm$ 6.2	>0.05
After one <i>B. ternarius</i> added		102.6 $\pm$ 5.5	

<sup>a</sup> One-tailed Wilcoxon Test.

Seventy percent of the combinations of bumble bees naturally occurring on goldenrod clusters were less extreme than the 3 *terricola*:1 *ternarius* ratio tested, and only 13 percent of the combinations were more extreme than this (Morse, unpublished data). These ratios suggest that *ternarius* may have avoided flower clumps upon which *terricola* were particularly dense, but I have not yet tested this possibility.

Simultaneous observations indicate that avoidance of *terricola* by *ternarius*, rather than overt aggression on the part of *terricola*, is the mechanism responsible for this partitioning. I have not observed bumble bees to attack each other on goldenrod, although I have seen such interactions on flowers and artificial food sources that provide individual rewards much greater than those of goldenrod (Morse MS). When they confronted large *terricola* head-on, the *ternarius* retreated rapidly. I made 4 such observations in the experiments. The *terricola* gave no obvious response at such times. These shifts do not result from *terricola* exploiting resources in areas that would otherwise be exploited by *ternarius* (Morse, 1977).

I have dealt here only with interactions between *ternarius* workers and large *terricola* workers. Relationships between small *terricola* workers and *ternarius* workers (which are all small) may reveal a different pattern, but I have not yet completed these experiments. Nevertheless, the results presented account for a large part of the possible interactions between the two species, because of the minimal overlap in size. As a result, these data go a long way toward assessing the importance of these two species on each other. The precision of this assessment should improve as I complete more parts of this picture (*ternarius* vs. small *terricola*). Since goldenrod is the primary food source for both *ternarius* and *terricola* in the study area during August, an estimate of their impact upon each other on goldenrod accounts for most of their interactions. Further, in the study area *ternarius* in large part concentrates on goldenrod, with the number of individuals seen on these flowers considerably exceeding the total seen on all other flowers during the summer. Thus, the interactions on goldenrod are a vital aspect of *ternarius*' existence.

#### Acknowledgments

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Department of Zoology, University of Maryland, College Park, MD 20742.